

## Ecological and cenotic features of the old-growth *Pinus sibirica* forests in the North-Chuya glaciation center, Russian Altai

E.E. Timoshok<sup>1\*</sup>, E.N. Timoshok<sup>1</sup>, I.I. Gureyeva<sup>2,3</sup>

<sup>1</sup>*Institute of Monitoring of Climatic and Ecological Systems SB RAS,  
Academicheskoye ave. 10/3, 634055, Tomsk, Russia*

<sup>2</sup>*Tomsk State University, Lenina ave. 36, 634050 Tomsk, Russia*

<sup>3</sup>*Tomsk Oil and Gas Design and Research Institute, Mira ave. 72, 634027 Tomsk, Russia*

\*Corresponding author E-mail: [timoshokee@mail.ru](mailto:timoshokee@mail.ru)

Received: 10.11.2020. Accepted 15.12.2020

Ecological and cenotic features of the old-growth forests of Siberian pine – *Pinus sibirica* Du Tour situated in the mountain-glacial basin Aktru in the North-Chuya glaciation center of the Russian Altai at the altitudes of 2160–2300 m a.s.l. were examined for the first time. These forests can be defined as virgin ones since they have never been subjected by direct human-caused disturbances throughout their existence. This makes them a valuable pattern of the undisturbed forests of the Altai. The age of the primary generation of *P. sibirica* forming the base of the tree layer of these forests is about 400 years; the age of some trees reaches 600 years and more. A significant floristic diversity (104 species of vascular plants) was detected in these forests. In the Aktru mountain-glacial basin, old-growth forests of *P. sibirica* exist in eight variants, significantly differing in the composition and structure of subordinate layers and the diversity of vascular plants, mosses, and ground lichens. We have carried out the phytosociological indication of the most important ecological factors at the old-growth *P. sibirica* forests situated on the northern, western, and eastern slopes of the valley of the Aktru River. Despite the fact, these forests are found on different types of soils (coarse-humus gleyed cryozems in the northern slope, typical soddy-podburs on the eastern one, and skeletal coarse-stony weak podburs in the western slope), all habitats are characterized by narrow ranges of moisture conditions – four grades (67.1 to 70.0) indicated series of humid-forest habitats and active soil richness – two grades (7.0 to 8.1) indicated series of mesotrophic habitats. Such environmental conditions are optimal for *P. sibirica* in all studied habitats. Both the great scientific significance of the examined old-growth *P. sibirica* forests for climatic and environmental studies and the need for their conservation, due to their rarity, undisturbed state, and significant age of the trees, are noted.

**Keywords:** old-growth forests; *Pinus sibirica*; phytosociological indication of habitats; North-Chuya center of glaciation; Russian Altai.

### Introduction

The study and protection of the still extant fragments of old-growth forests, mainly coniferous-deciduous, has been given special attention in Western and Eastern Europe since the end of the 20<sup>th</sup> or the beginning of the 21<sup>st</sup> century (Peterken, 1996; Lindholm, 1999; Pullin, 2002; East European Forests, 2004; Angelstam et al., 2011). An extensive literature is devoted to the South Siberian mountain forests and forest-forming species, including Siberian pine – *Pinus sibirica* Du Tour. In different regions, the floristic composition and types of forests, environmental factors of the distribution of the main forest-forming species and their ecological features, features of renewal, the role of climatic and phytocenotic factors in the formation of forests were studied, and generalizing works were published (Tipy lesov..., 1980; Krylov et al., 1983; Kedrovye ..., 1985; Polikarpov et al., 1986 and many others). However, old-growth forests, due to their rare occurrence, remain insufficiently studied to date.

The World Wildlife Fund (WWF) has included the Altai-Sayan mountainous country in the list “Global 200”. This list includes the most valuable virgin or slightly modified ecoregions of the Earth, where more than 90 % of the world's biodiversity is concentrated, for the conservation of which ecological studies of unique landscapes are of priority importance. Sporadic fragments of old-growth forests that have been preserved in the Altai Mountains should be confidently attributed to such unique ecosystems.

The study of the Altai forests conducted in the 50 to the 60s of the 20<sup>th</sup> century (Kuminova, 1960; Krylov, Rechan, 1965) showed that forests from *Pinus sibirica* with shrub-green-mosses and herb-ferns cover are widespread in the Priteletsky Altai (800–1500 m a.s.l.). The Siberian pine forests with *Betula rotundifolia*+lichen+green moss and herbal cover are common on the eastern, northern, and western ridges of the Altai (1800–2000 m a.s.l.). In these forests, the trees of *P. sibirica* are 100–200, rarely about 300 years old. A.V. Kuminova (1960) mentioned the only fragment of the nemoral forest of *Pinus sibirica* with the admixture of *Abies sibirica* Ledeb. and dense large-herb-fern ground cover growing on the brown forest soil in the low mountains of the Priteletsky Altai (Kyga River, 500 m a.s.l.), where some *Pinus sibirica* trees reach more than 500 years old.

E.A. Zhukov (2006) noted that old *Pinus sibirica* and *Larix sibirica* trees (age over 400 years) are less and less common in most forest landscapes of the Altai-Sayan region. Therefore the single autochthonous forest fragments, where the specimens of old trees occur, are of great interest.

At the beginning of the 21<sup>st</sup> century, *Pinus sibirica* forests located in the upper reaches of the Aktru River (mountain-glacial basin Bish-lirdu, North-Chuya center of glaciation) have been examined at an altitude more than 2160 m a.s.l. The tree layer of these forests includes *P. sibirica* trees of four generations with the average ages of 410–490 years (the main generation), 220–360 years, 90–190 years, and 50–80 years. Furthermore, single *P. sibirica* trees of 650–730, and even 830 years old are found in these forests (Vorobyov et al., 2001; Bocharov, 2011; Timoshok et al., 2016).

The expressed diversity of tree ages, the presence of renewal sites, a large number of dead trees of varying degrees of decomposition, and great floristic diversity of 104 species of vascular plants (Timoshok et al., 2009, 2010), which makes up almost a half of the whole flora of *Pinus sibirica* forests the Russian Altai (236 species, according to Kuminova, 1960), allows us to classify these forests as old-growth and virgin ones. B.A. Ivashkevich (1929) gave the following definition of virgin forests: these are forests that existed before and now exist without human disturbances, which are characterized by different ages of trees, periodicity of natural renewal, group placement of trees, and undergrowth by the area. Currently, the forests are considered to be virgin if they have reached the climax stage and have not been affected by human and natural destructive factors or only indirectly influenced by humans (Komin, 2017).

This work aims to identify the floristic diversity, cenotic and ecological originality of old-growth *Pinus sibirica* forests in the North-Chuya glaciation center at the upper limit of their distribution in the Russian Altai (2160–2300 m a.s.l.) represented a standard of undisturbed forest ecosystems and having the special value for the study of their dynamics and stability.

## Materials and methods

The studies were carried out in old-growth *Pinus sibirica* forests growing in the upper reaches of the Aktru River (50°05' N, 87°45' E). The Aktru basin lies in the Bish-lirdu mountain massif in the highest part of the North-Chuya Ridge. This mountain-glacial massif is located in a zone of high-mountain dissected relief, composed of a moraine cover of different ages, which is dominated by strongly dislocated sericite-chlorite slates with an admixture of quartzites. Moraines of the Malyi and Bolshoi Aktru glaciers descend into the valley (Dushkin, 1967). The climate here is severe alpine: the annual average temperature is –5.2 °C, the daytime average temperature in June to August is +8.7 °C; the long-term average annual precipitation is 520 mm, with about 75 % of this amount falling during the warm period from May to September (Ledniki ..., 1987; Sevast'yanov, 1998). The growing season is short: 40–50 days with temperatures above +10 °C, the sum of active temperatures at an altitude of 2150 m a.s.l. is about 600 °C, and about 500 °C at the upper boundary of closed forests (2300 m a.s.l.); the relative humidity is high, about 70 %. In July, the temperature often drops to 0 ... +4 °C at night, and it rises to +15 ... +18 °C in the daytime. June and August's night temperatures are often subzero, the daytime temperatures are +14 ... +15 °C. The average amplitude of the daily course of air temperature in June and August is about 12 °C. This contrast between nighttime and daytime temperatures, combined with high air humidity, leads to strong nighttime condensation and copious dew.

The study of old-growth *Pinus sibirica* forests have been carried out for 15 years (1999–2014) on the high-altitude ecological transect located in the lower parts of the northern, western, and eastern slopes of the Aktru River valley and stretched from the lower (2160 m a.s.l.) to upper (2300 m a.s.l.) border of forest distribution. The total area of the studied *P. sibirica* forests is about 4 km<sup>2</sup>. About 70 complete geobotanical descriptions with detailed characteristics of all plant layers have been made: the arboreal, shrub, herb-dwarf shrub, and moss-lichen layers. The projective coverage (in percentages) was estimated for whole herb-dwarf shrub cover (the total projective coverage, TPC), and for each species of vascular plants, mosses, and ground lichens, as well as for each layer. The crown closure of the tree layer we indicate in shares of 1.

Geobotanical descriptions were processed with using of the Integrated Botanical Information System (IBIS) (Zverev, 2007) developed on the base on the standard ecological scales of Ramenskiy-Tsatsenkin (Ramensky et al., 1956; Tsatsenkin, 1967; Tsatsenkin et al., 1978) to assess the habitats of old-growth *Pinus sibirica* forests on the most important abiotic factors such as moisture and active soil richness.

The spelling of the scientific names of plants and abbreviations of the authors' names were corrected according to "IPNI. International Plant Name Index" (<https://www.ipni.org/>), the species authors names are shown in Table 1.

## Results and discussion

Studies have shown that unique survived old-growth *Pinus sibirica* forests are located in the valley of the Aktru River above the vast fields of stony placers, which provided their long-term preservation from fires. Below these stone fields in the mountain forest belt of the North-Chuya Ridge from the altitude 2160 m a.s.l., young larch forests are predominated, which are renewed after the fires of the middle to the end of 19<sup>th</sup> century, recorded in this territory in 1898 by Professor V.V. Sapozhnikov (1901) (Timoshok et al., 2016).

Three fragments of old-growth *Pinus sibirica* forests separated from each other by young moraines of the Malyi Aktru glacier are revealed in periglacial zone on gentle (3–5°) northern slopes at altitude of 2200–2300 m a.s.l. These fragments are located near the young moraines of this glacier in the current regressive phase of the Little Ice Age. These forests were located in close proximity to the glacier during significant cooling of the climate and the onset of the glacier during the Little Ice Age (about 400 years from the end of the 14<sup>th</sup> century to the middle of the 19<sup>th</sup> century) (Okishev et al., 2000). Under the environmental conditions of the periglacial zone on the northern slope, the tree layer of old-growth forests is formed only by *Pinus sibirica* (100 %). Here we have been identified three types of Siberian pine forests: (1) with a ground cover of *Vaccinium vitis-idea*+*Bergenia crassifolia*+green mosses, (2) with a ground cover of *Betula rotundifolia*+grass+lichen+green mosses, and (3)

with a ground cover of *Betula rotundifolia*+green mosses depending on the peculiarities of the mesorelief and the crown closure of the tree layer in the periglacial habitats.

(1) *Pinus sibirica* forests with a ground cover of *Vaccinium vitis-idea*+*Bergenia crassifolia*+green mosses occupy the tops and slopes of stony manes. The crown closure of the tree layer is medium (0.4–0.5). The floristic diversity of these forests is greatest: 39 species of vascular plant, eight species of mosses, and three species of ground lichens (Table 1). The shrubs – *Betula rotundifolia*, *Juniperus sibirica*, *Lonicera altaica*, *L. hispida*, *Salix glauca* grow sporadically and do not form a closed layer: they sum projective coverage is about 5 %. The well-developed herb–dwarf shrub layer (34 species, TPC about 40 %) is dominated by *Bergenia crassifolia* (20 %) and *Vaccinium vitis-idaea* (10 %); other species – *Empetrum nigrum*, *Festuca altaica*, *Poa altaica* etc. participate with low projective coverage. Green mosses – *Hylocomium splendens*, *Pleurozium schreberi*, and *Stereodon revolutus* prevail in the well-developed moss-lichen layer (projective coverage 40 %).

(2) *Pinus sibirica* forests with a ground cover of *Betula rotundifolia*+grass+lichen+green mosses occupy the flattened sites on the slopes. They are characterized by low crown closure of tree layer (0.2–0.3) and relatively great floristic diversity of the ground layer: 34 species of vascular plants, eight species of green mosses, and one species of ground lichens have been recorded in these forests (Table 1). *Betula rotundifolia* (20 %) predominates in the well-developed shrub layer (projective coverage 30 %), with *Juniperus sibirica* and *Lonicera altaica* taking a prominent part. In the herb–dwarf shrub layer (29 species, TPC about 30 %), *Calamagrostis pavlovii* (10–12 %) and *Vaccinium vitis-idaea* (5–7 %) are the most abundant, other species – *Aegopodium alpestre*, *Bergenia crassifolia*, *Carex macroura*, *Festuca altaica*, *Poa sibirica*, etc. have lower projective coverage. Lichen *Cladonia stellaris*, and mosses *Hylocomium splendens* and *Pleurozium schreberi* are co-dominants in the well-developed moss-lichen layer (projective coverage 50 %).

(3) *Pinus sibirica* sparse forests with a ground cover of *Betula rotundifolia*+green mosses occupy the relief depressions. The trees of *P. sibirica* do not form a well-defined layer, their crown closure is 0.1. In such forests, there is numerous deadwood of Siberian pine with a diameter of 1 m and more, indicating that the tree layer was more closed in the recent past. 29 species of vascular plants, five species of mosses, and three species of ground lichens have been recorded in such forests (Table 1). The shrub layer is dense (projective coverage 70 %) with *Betula rotundifolia* (60 %) dominating it; *Salix saposhnikovii*, *S. glauca*, and *Lonicera altaica* are less abundant. The herb–dwarf shrub layer includes 24 species (TPC 7–10 %); projective coverage of separate species is very low, except for *Carex sabyrensis* (3–5 %). Moss *Hylocomium splendens* dominates in the moss layer (projective coverage about 80 %), with a significant abundance of *Aulacomnium palustre* and *Dicranum spadicum*.

All Siberian pine forests in periglacial zone on the northern slope are confined to coarse-humus gleyed cryozems thawing to a depth of 40–60 cm by mid-July with permafrost locates below (Davydov & Timoshok, 2010). In these environmental conditions, the habitats of Siberian pine in old-growth forests are characterized by a 4-grade range of moisture conditions (grades 67.1 to 70.0), according to Ramensky–Tsatsenkin scales. The lowest values of this indicator (grades 67.1 to 68.1) are characteristic of *Pinus sibirica* forests (1) with a ground cover of *Vaccinium vitis-idea*+*Bergenia crassifolia*+green mosses located on the tops and slopes of stony manes; slightly higher moisture content is in forests (2) with a ground cover of *Betula rotundifolia*+grass+lichen+green mosses on the flattened sites on the slopes (grades 69.3 to 69.6), sparse *Pinus sibirica* forests (3) with a ground cover of *Betula rotundifolia*+green mosses located in mesorelief depressions occupy the habitats with higher moisture content (grades 69.5 to 70).

Analysis of data on the second most important abiotic factor – active soil richness – showed that periglacial habitats of Siberian pine forests have a narrow 1.5-grade range of active soil richness (grades 7.0 to 7.6). The habitats of old-growth Siberian pine forests are poorly differenced for this factor in ecological conditions of periglacial zone. The range of active soil richness is 7.1 to 7.2 grades in *P. sibirica* forests (1), 7.1 to 7.6 grades in *P. sibirica* forests (2), and 7.0 to 7.3 grades in *P. sibirica* forests (3).

The valley old-growth *Pinus sibirica* forests are located on the eastern (10–20°, 2180 m a.s.l.) and western (5–15°, 2160 m a.s.l.) slopes of the valley of Aktru River, in 300 and 1100 m respectively from the terminal moraine line of the Malyi Aktru glacier. These forests were at the same distance from the advancing glacier in the Little Ice Age.

In the forests on the eastern slope, only Siberian pine (100 %) forms a tree layer. Two types of forests have been recorded here: (4) with grass+*Vaccinium vitis-idea*+green mosses cover and (5) with *Lonicera altaica*+green mosses cover.

(4) *Pinus sibirica* forests with a ground cover of grass+*Vaccinium vitis-idea*+green mosses are characterized by medium crown closure of tree layer (0.4–0.6) and relatively low floristic diversity of the ground cover: 21 species of vascular plants, seven species of mosses, and one species of ground lichens (Table 1). The shrub layer is not formed. The herb–dwarf shrub layer includes 20 species (TPC 40 %) with a dominating of *Vaccinium vitis-idaea* (projective coverage about 15 %), and significant participation of *Calamagrostis pavlovii*, *Poa sibirica*, *Carex macroura*, and *Aconitum altaicum*. The mosses *Hylocomium splendens* and *Rhytidium rugosum* prevail in the moss cover (projective coverage 60 %).

(5) *Pinus sibirica* forests with a ground cover of *Lonicera altaica*+green mosses have sparse tree layer characterized by low crown closure (0.1–0.2). The floristic diversity of the ground cover is lower than in the forest (4): 19 species of vascular plants, seven species of mosses, and one species of lichens (Table 1). The well-developed shrub layer (projective cover approximately 60 %) is formed mostly by *Lonicera altaica* (projective coverage about 50 %). In the herb–dwarf shrub layer (15 species, TPC 20 %), *Calamagrostis pavlovii* dominates (10 %); participation of *Poa sibirica*, *Aconitum leucostomum*, *Geranium albiflorum*, *Vaccinium vitis-idaea* is less significant. The mosses *Hylocomium splendens* and *Rhytidium rugosum* dominate the moss cover (projective coverage 60 %).

The typical soddy-podburs without permafrost are developed under the *Pinus sibirica* forests on the well-drained eastern slope (Davydov, Timoshok, 2010). The habitats of these forests are characterized by a 2.5-grade range of moisture conditions (grades 67.5 to 68.9). In forests (5) with *Lonicera altaica*+green mosses cover, the moisture conditions are one grade higher (grades 68.1 to 68.9) than in forests (4) with grass+*Vaccinium vitis-idea*+green mosses cover (grades 67.5 to 67.9). The range of the active soil richness in environmental conditions of the eastern slope is also narrow – 1.5 grade (7.6 to 8.1), but the habitats here are on

this factor slightly, one grade higher than that in the periglacial zone. Eastern slope habitat differences between *Pinus sibirica* forests are insignificant: 7.6 to 7.8 grades in forests (5) and 7.7 to 8.1 grades in forests (4).

In the conditions of the western slope, Siberian larch (20 %) is added to the dominant Siberian pine (80 %) in the tree layer. At present, old-growth *Pinus sibirica* forests have a low density here (crown closure 0.1–0.2), but the numerous large deadwood of *P. sibirica* of the different degrees of decomposition show that tree layer density was higher here in the recent past. We have identified on the western slope three types of *P. sibirica* forests: (6) with *Festuca+Calamagrostis+green mosses+lichens* cover, (7) with *Bergenia crassifolia+Empetrum nigrum+lichens* cover, and (8) with grass+*Vaccinium vitis-idea+lichens* cover.

(6) *Pinus sibirica* forests with a ground cover of *Festuca+Calamagrostis+green mosses+lichens* occupy fine-stony sites of the slope. Ground cover is characterized by low floristic diversity: 19 species of vascular plants, five species of mosses, one species of ground lichens (Table 1). The separate individuals of shrubs *Lonicera altaica*, *L. hispida*, *Juniperus sibirica*, *Salix sajanensis*, *S. saposhnikovii* do not form a closed layer. The well-developed herb-dwarf shrub layer (14 species, TPC 30–40 %) is dominated by *Calamagrostis pavlovii* (20 %) and *Festuca altaica* (10 %); *Bistorta vivipara*, *Carex sabyensis* and others have low projective coverage. In the well-developed moss-lichen layer (projective coverage 80 %), the lichen *Cladonia stellaris* (50 %) dominates, with significant participation of mosses *Hylocomium splendens* and *Sanionia uncinata*.

(7) *Pinus sibirica* forests with a ground cover of *Bergenia crassifolia+Empetrum nigrum+lichens* are located on gentle (3–5°) medium-stony sites of the slope. They are characterized by the lowest floristic diversity: 14 species of vascular plants, two species of mosses, and one species of ground lichens (Table 1). These forests have not shrub layer. The well-developed herb-dwarf shrub layer is dominated by *Empetrum nigrum* (20 %) and *Bergenia crassifolia* (10 %); dwarf shrub *Vaccinium vitis-idaea* and grass *Festuca altaica*, *F. sphagnicola* and others have low participation there. The lichen *Cladonia stellaris* (30 %) predominates in well-developed moss-lichen layer; moss *Rhytidium rugosum* has also a significant participation here.

(8) *Pinus sibirica* forests with a ground cover of grass+green mosses+lichens are located on the steep (15–20°) large-stony-blocky sites of the slope. They are characterized by medium floristic diversity: 22 species of vascular plants, five species of mosses, and one species of ground lichens. Shrub species *Lonicera altaica*, *L. hispida*, and *Salix sajanensis* do not form a layer, they grow as separate individuals. The herb-dwarf shrub layer formed by 19 species (TPC 20 %) in niches between large stones and boulders is patchy. The most significant participation is recorded for grass species *Anthoxanthum alpinum*, *Festuca sphagnicola*, *F. altaica*, *F. tristis* (the sum projective coverage is about 15 %). These plants represent the collective dominant there. The herb *Aegopodium alpestre*, and dwarf shrub *Vaccinium vitis-idaea* have low projective coverage. In the moss-lichen layer (projective coverage 30 %), the lichen *Cladonia stellaris* (15–50 %) and moss *Pleurozium schreberi* dominate.

Under the *Pinus sibirica* forests of the western slope, skeletal coarse-stony weak podburs are developed. The range of moisture of the habitats of *Pinus sibirica* forests on this slope is 2.5 grades (66.7 to 68.1). The drier habitats are occupied by the forests (6) with *Festuca+Calamagrostis+green mosses+lichens* cover (grades 66.7 to 67.6) and the forests (8) with grass+green mosses+lichens cover (grades 66.8 to 67.1). The moisture of the forests (7) with *Bergenia crassifolia+Empetrum nigrum+lichens* cover is slightly higher (grades 67.1 to 68.1). The range of active soil richness under *P. sibirica* forests on the western slope is also narrow and amounts to 1.5 grades (7.0 to 7.7). For this factor, the habitats differ slightly: this indicator is 7.5–7.6 grades in the forests (6), 7.0–7.5 grades in the forests (7), and 7.3–7.7 grades in the forests (8).

All examined old-growth *Pinus sibirica* forests are ecologically confined to the lateral moraines of the Aktru glacier of the Akkem stage. The tongue of this glacier occupied the entire upper part of the river valley about 4 thousand years ago and had a thickness of 200 m (Dushkin, 1967). On these moraines, massifs of old-growth cedar forests developed autochthonously as the glacier of the Akkem stage retreated. In the tree layer of these forests, the main generation is dominated by *P. sibirica* trees more than 400 years old, and the age of some trees reaches 700 and even 800 years. A great number of large *P. sibirica* deadwood of various degrees of decomposition is recorded. The tree layer of the studied forests in two locations – in the periglacial one on the northern slope and the valley on the eastern slope – consists exclusively of *P. sibirica*; *Larix sibirica* is mixed with it on the western slope.

Among the examined *Pinus sibirica* forests, the forests located in the periglacial zone on the northern slope are characterized by a higher floristic diversity of vascular plants. The number of species varies here from 29 in the forests (3) with *Betula rotundifolia+green moss* cover to 39 species in the forests (1) with *Vaccinium vitis-idea+Bergenia crassifolia+green moss* cover. In the valley, *P. sibirica* forests, both on the eastern and western slopes, the floristic diversity of vascular plants is 1.5–2 times lower. It should be noted that only three species of vascular plants are found in the ground cover of all examined forests – *Lonicera altaica*, *Vaccinium vitis-idaea*, and *Calamagrostis pavlovii*, the rest of the species are specific for each forest. The greatest number of specific species – 13, are recorded under the conditions of the northern slope in the periglacial zone, including vascular plants *Salix glauca*, *S. vestita*, *Carex tristis*, *Hedysarum neglectum*, *Pedicularis brachystachys*, *P. incarnata*, *Poa altaica*, *Saussurea parviflora*, mosses *Polytrichum juniperinum*, *Stereodon revolutus*, and ground lichens of the genus *Cladonia* (Table 1). In the forests located in the upper part of the Aktru River valley, the number of specific species is much less. Seven specific species: vascular plants *Aconitum altaicum*, *A. leucostomum*, *Pedicularis elata*, *Pleurospermum uralense*, *Trifolium lupinaster* and mosses *Brachythecium rivulare*, *Polytrichum strictum* occur in the forests on the eastern slope of the valley. Only five specific species grow in the forests on the western slope, there are: *Larix sibirica*, *Salix sajanensis*, *Antennaria dioica*, *Festuca sphagnicola*, *Pedicularis compacta* (Table 1).

Surprisingly, ferns are found in the examined high-mountain old-growth *Pinus sibirica* forests neither on stony substrates nor on the soil. At the same time, eight fern species occur on stony placers, young and old moraines (Gureyeva, Timoshok, 2016) located above and below these forests.

**Table 1.** Species composition and the projective cover of the main species of vascular plants, mosses and lichens in the old-growth *Pinus sibirica* forests at the upper limit of their distribution in the North-Chuya glaciation center (Aktru River valley)

Species composition	Northern slope, periglacial zone			Eastern slope		Western slope		
	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)
<b>High shrub layer</b>								
<i>Betula rotundifolia</i> Spach	2-3	20	60	-	3-5	-	-	-
<i>Juniperus sibirica</i> Burgsd.	S	3-5	S	-	S	1-2	<1	<1
<i>Lonicera altaica</i> Pall.	1-2	3-5	1-2	S	50	5	S	<1
<i>Lonicera hispidula</i> Pall. ex Schult.	S	-	-	-	S	S	-	-
<i>Salix glauca</i> L.	S	S	1-2	-	-	-	-	-
<i>Salix sajanensis</i> Nasarow	-	-	-	-	-	S	-	S
<i>Salix saposchnikovii</i> A.K. Skvortsov	-	S	3-5	-	-	S	-	-
<b>Herb-dwarf shrub layer</b>								
<i>Aconitum altaicum</i> Steinb.	-	-	-	5	-	-	-	-
<i>Aconitum decipiens</i> Vorosch. et Anfalov	S	S	-	-	<1	-	-	-
<i>Aconitum leucostomum</i> Vorosch.	-	-	-	1	1-3	-	-	-
<i>Aegopodium alpestre</i> Ledeb.	<1	1-2	S	1-3	S	<1	-	1-2
<i>Antennaria dioica</i> (L.) Gaertn.	-	-	-	-	-	-	-	S
<i>Anthoxanthum alpinum</i> Á. Löve et D. Löve	S	S	S	-	-	S	-	5
<i>Bergenia crassifolia</i> (L.) Fritsch	20	1-2	1	-	-	-	10	1
<i>Bistorta major</i> Gray	-	<1	-	<1	<1	-	-	-
<i>Bistorta vivipara</i> (L.) Gray	<1	<1	<1	S	-	1-2	-	1
<i>Calamagrostis pavlovii</i> (Roshev.) Roshev	<1	10	<1	5-7	10	20	<1	<1
<i>Carex macroura</i> Meinsh.	S	2-3 %	-	5 %	-	-	<1	-
<i>Carex sabyensis</i> Less. ex Kunth.	S	-	3-5	-	-	1-3	-	<1
<i>Carex tristis</i> M. Bieb.	S	<1	-	-	-	-	-	-
<i>Cerastium pauciflorum</i> Turcz. ex Steud.	S	<1	-	S	S	<1	-	-
<i>Cicerbita azurea</i> Beauverd	S	S	S	S	S	-	-	-
<i>Delphinium elatum</i> L.	S	S	-	S	-	-	-	-
<i>Dianthus superbus</i> L.	-	S	-	S	-	-	-	-
<i>Empetrum nigrum</i> L.	1-3	S	-	-	-	-	20	1
<i>Festuca altaica</i> Trin.	2-3	1-2	1-2	-	-	10	1-2	2-3
<i>Festuca sphagnicola</i> B. Keller	-	-	-	-	-	-	2-3	5
<i>Festuca tristis</i> Krylov et Ivanitzk.	<1	-	-	-	-	S	S	1-2
<i>Gentiana grandiflora</i> Laxm.	S	S	S	-	-	-	S	-
<i>Geranium albiflorum</i> Ledeb.	-	S	<1	<1	1-2	-	-	-
<i>Hedysarum neglectum</i> Ledeb.	1	<1	S	-	-	-	-	-
<i>Linnaea borealis</i> L.	S	-	-	-	-	-	<1	S
<i>Trifolium lupinaster</i> L.	-	-	-	S	S	-	-	-
<i>Luzula parviflora</i> Desv.	S	S	-	-	-	S	-	-
<i>Luzula sibirica</i> V.I. Krecz.	S	S	S	S	S	-	-	-
<i>Moehringia umbrosa</i> Fenzl	S	-	S	-	-	-	-	-
<i>Pedicularis brachystachys</i> Bunge	-	S	S	-	-	-	-	-
<i>Pedicularis compacta</i> Stephan ex Willd.	-	-	-	-	-	S	S	S
<i>Pedicularis elata</i> Willd.	-	-	-	S	S	-	-	-
<i>Pedicularis incarnata</i> L.	S	S	S	-	-	-	-	-
<i>Pleurospermum uralense</i> Hoffm.	-	-	-	<1	S	-	-	-
<i>Poa altaica</i> Trin.	2-3	<1	-	-	-	-	-	-
<i>Poa sibirica</i> Roshev.	<1	2-3	S	3-5	3-5	<1	-	-
<i>Poa urssulensis</i> Trin.	<1	-	-	<1	S	-	-	-
<i>Potentilla gelida</i> C.A.Mey.	S	-	S	-	-	-	-	S
<i>Pyrola incarnate</i> Fisch. ex DC.	S	S	-	S	-	-	S	-

<i>Salix vestita</i> Pursh	<1	<1	<1	-	-	-	-	-
<i>Saussurea parviflora</i> (Poir.) DC.	S	-	S	-	-	-	-	-
<i>Swertia marginata</i> Schrenk	<1	S	S	-	-	S	-	-
<i>Stellaria peduncularis</i> Bunge	-	S	-	-	-	S	-	-
<i>Tephrosieris integrifolia</i> (L.) Holub	S	-	-	-	-	-	-	S
<i>Thesium repens</i> Ledeb.	-	-	S	-	-	-	-	S
<i>Vaccinium vitis-idaea</i> L.	7-10	5-7	<1	15	1-2	1	2-3	1-2
<i>Veratrum lobelianum</i> Bernh.	S	-	S	-	-	-	-	S
<i>Viola altaica</i> Ker Gawl.	S	-	S	-	-	-	-	S
<b>Moss-lichen layer</b>								
<i>Aulacomnium palustre</i> (Hedw.) Schwägr.	-	S	15	-	-	S	-	S
<i>Dicranum spadicum</i> J.E. Zetterstedt	2-3	S	10	S	S	S	-	-
<i>Hylocomium splendens</i> W.P. Schimper	10	10	40	30	30	15	-	2-3
<i>Pleurozium schreberi</i> Mitten	10	10					3	10
<i>Polytrichum juniperinum</i> Hedwig	1-2	5	1-2	-	-	-	--	-
<i>Polytrichum strictum</i> Menzies ex Bridel	-	-	-	5	5	-	-	-
<i>Rhytidium rugosum</i> Kindberg	1-2			20	15	5	10	2-3
<i>Sanionia uncinata</i> Loeske	2-3	S	2-3	5	10	10	-	S
<i>Stereodon revolutus</i> Mitt.	10	5	-			-	-	-
<i>Cladonia stellaris</i> (Opiz) Pouzar et Vězda	5	20	3-5	-	-	50	30	15

**Notes:** Numbers in the columns means the projective coverage in %; 'S' means that species is present by singular exemplars; '-' means absence of the species. Numbers at the head of each column (1 to 8) refer to the variant of the examined forests of *Pinus sibirica*: **Northern slope:** (1) - with *Vaccinium vitis-idea*+*Bergenia crassifolia*+green moss cover; (2) - with *Betula rotundifolia*+grass+lichen+green moss cover; (3) - with *Betula rotundifolia*+green moss cover; **Eastern slope:** (4) - with grass+*Vaccinium vitis-idea*+green moss cover; (5) - with *Lonicera altaica*+green moss cover; **Western slope:** (6) - with *Festuca*+*Calamagrostis*+green moss+lichen cover; (7) - with *Bergenia crassifolia*+*Empetrum nigrum*+lichen cover; (8) - with grass+green moss+lichen cover.

The examined *Pinus sibirica* forests differ from each other not only in their species composition but also in the specificity of their cenotic structure. The shrub layer has a different development in forests located in the periglacial zone on the northern slope depending on the crown closure of the tree layer, mesorelief, and stoniness of the substrate, from its absence in forests with a medium crown closure of the tree layer on the tops and slopes of stony manes to a well-developed one with the dominance of *Betula rotundifolia* in sparse forests located in the relief depressions. An inverse dependency was noted for the development of the herb-dwarf shrub layer from crown closure and density of shrub layer: in the sparse forests with shrub layer dominated by *Betula rotundifolia* (60-70 % of the projective coverage), the herb-dwarf shrub layer is sparse (7-20 % of the projective coverage), while in forests with the medium crown closure of tree layer and no or sparse shrub layer, the herb-dwarf shrub layer is denser (to 30-40% of the projective coverage). We also observed a change in the dominants of the herb-dwarf shrub layer depending on the mesorelief and stony of the substrate in the periglacial zone: *Bergenia crassifolia* prevails on stony manes, *Calamagrostis pavlovii* predominates in flat areas, and in the mesorelief depressions dominant species are absent. There are also differences in the moss-lichen cover: although *Hylocomium splendens* has been significantly involved in all Siberian pine forests of this zone, *Pleurozium schreberi* and *Stereodon revolutus* occur in forests located on stony mane; both *Aulacomnium palustre* and *Dicranum spadicum* occur in sparse forests located in mesorelief depressions.

In contrast to the periglacial *Pinus sibirica* forests of the northern slope, the differences in the composition and structure of the shrub and herb-dwarf shrub layers of the forests on the eastern slope are mostly determined by the canopy density of the tree layer. *Lonicera altaica* prevails in the shrub layer, and *Calamagrostis pavlovii* predominates the herb-dwarf layer in sparse forests. The shrub layer is absent in forests with medium crown closure, and *Vaccinium vitis-idaea* prevails in the herb-dwarf shrub layer. In the conditions of the eastern slope, there are no significant differences in the composition and abundance of the dominants of the moss layer in the sparse forests and in forests with medium crown closure of tree layer.

The most dramatic differences in the composition and abundance of dominant species we found in the herb-dwarf shrub layer in Siberian pine forests with an absent or unexpressed shrub layer growing under the ecological conditions of the western slope of Aktru River valley. *Calamagrostis pavlovii* and *Festuca altaica* predominate in the herb-dwarf shrub layer in forests growing on gentle fine-stony slopes; *Empetrum nigrum* and *Bergenia crassifolia* prevail in forests growing on medium-stony substrates; and Gramineae species *Anthoxanthum alpinum*, *Festuca sphagnicola*, *F. altaica*, *F. tristis* are collective dominant in forests located on the steep large-stony-blocky sites of the slope. The lichen species *Cladonia stellaris* dominates the moss-lichen layer of all three types of *Pinus sibirica* forests on the western slope.

In all of the examined *Pinus sibirica* forests with a high density of the shrub layer, the sparseness of the herb-dwarf shrub layer is probably associated with a lower illumination under the shrub canopy. Permafrost does not affect the development of the herbaceous layer. In the absence of a shrub layer, the herb-dwarf shrub layer is well-developed (projective coverage 40 %) both on permafrost soil under the periglacial forests on the northern slope and soil without permafrost under the forests on the eastern and western slopes of Aktru River valley.

Our studies have shown, that in the oroclimatic conditions of the North-Chuya center of glaciation, all the habitats of old-growth *Pinus sibirica* forests occupy a 4-grade range of moisture supply (grades 67.1 to 70.0), which corresponds to the wet-forest series of habitats, and 2-grade range of active soil richness (grades 7.0 to 8.1) which corresponds to the series of mesotrophic habitats. The greatest moisture supply is characteristic of the habitats of the periglacial *P. sibirica* forests on the northern slopes; moisture is somewhat lower in the habitats on the western slope; the habitats of the eastern slope are intermediate. As regards the factor of active soil richness, the differences are even less significant. All habitats for these most important environmental factors are in the optimum range of the *P. sibirica*, indicated earlier for this species in the Aktru River basin (Timoshok et al., 2014) as 67–71 grades on moisture supply and 7.0–8.5 grades on the active soil richness. On the whole, the ranges of the variability of these indicators in *P. sibirica* forests, autochthonously formed on the moraine cover of the glacier of Akkem stage, are small, which is apparently due to the similarity of the parent rock with the predominance of sericite-chlorite shales, and the temperature regime of the habitats.

The different types of soils are formed under the *Pinus sibirica* forests on different slopes in various conditions of the relief and microclimate: coarse-humus gleyed cryozems are formed in the conditions of the northern slope, soddy-podburs are formed on the well-drained eastern slope, and skeletal coarse-stony weak podburs are formed on the western slope. Close values of ranges of moisture and active soil richness are caused by a large amount of precipitation, high air humidity, a large difference of night and daytime temperatures, which is the cause of significant night condensation of moisture (copious dew), different thermal conditions of slopes of different orientations, weak formation and low soil thickness on moraines of the Akkem stage. The sum of active temperatures at altitudes of 2150–2300 m a.s.l. in the upper reaches of the Aktru River is 500 to 600 °C. This allows us to conclude that the *Pinus sibirica* forests in these oroclimatic conditions grow in the range of dominance of *P. sibirica*, determined earlier for the mountains of South Siberia as 350 to 800 °C (Polikarpov et al., 1986).

Furthermore, the range of environmental conditions of habitats of old-growth *Pinus sibirica* forests, calculated for the moisture and active soil richness using the Ramenskiy-Tsatsenkin scales, is included in the calculated range of optimal conditions for their edificatory species – *P. sibirica* (Timoshok et al., 2014). Existing in optimal conditions, apparently, determines a significant lifespan of *P. sibirica* trees up to 570, rarely up to 650–730 (830) years, and a long duration of their generative period, which lasts more than 500 years (Timoshok et al., 2009). Thus, the entire set of favourable environmental factors determines the stable existence and long-term, for many centuries, autochthonous development of old-growth *P. sibirica* forests in the upper reaches of the Aktru River at the upper forest line at altitudes of 2160–2300 m a.s.l., including the immediate vicinity of glaciers. It is striking that Siberian pine forests, significantly different in cenotic structure, were formed in similar oroclimatic conditions with slightly different indicators of the moisture and active soil richness on slopes of different orientations and steepness. Occupying a small total area (about 4 km<sup>2</sup>), they have significant differences in the floristic composition and abundance of dominant species of vascular plants, mosses, and lichens, and in the projective coverage of all subordinate layers. The high cenotic diversity of old-growth cedar forests is determined, first of all, by the duration of their existence (more than 600 years) and the significant spatial and microclimatic heterogeneity of the habitats they occupy.

The examined old-growth *Pinus sibirica* forests in the North-Chuya center of present-day glaciation that were not affected by the fires being in the Altai in the second half of the 19<sup>th</sup> century have great scientific importance as a standard of old-growth virgin forests of the Russian Altai. These forests can be an object for integrated climate and environmental research, as well as monitoring biodiversity at the regional and state levels (Convention., 1992). Their significance is because the age of the main generation of *P. sibirica* in these forests reaches 400 years or more, while *P. sibirica* trees older than 400 years are rarely found in the most forest of the Altai-Sayan region. The need to preserve high-mountain Altaian old-growth *P. sibirica* forests is caused to their uniqueness, undisturbed and significant age of trees. The inclusion of descriptions of these forests in the next editions of the “Green Book of Siberia” and the “Green Book of Russia” will promote their conservation.

## Acknowledgements

The study was carried out within the framework of the project of Siberian Branch of Russian Academy of Science, No. VIII.77.1.3 (E.E. Timoshok & E.N. Timoshok, Institute of Monitoring of Climatic and Ecological Systems), and within the framework of the State assignments of the Ministry of Science and Higher Education of the Russian Federation, project No. 0721-2020-0019 (I.I. Gureyeva, Tomsk State University).

## References

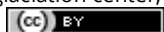
- Angelstam, P., Andersson, K., Axelsson, R., Elbakidze, M., Jonsson, B.G., Roberge, J.-M. (2011). Protecting forest areas for biodiversity in Sweden 1991–2010: the policy implementation process and outcomes on the ground. *Silva Fennica*, 45 (5), 1111–1133.
- Bocharov, A.Yu. (2011) Structure and dynamics of high-mountain forests of the (Severo-Chuyskiy Range, Mountain Altai) in the conditions of climate change. *Vestnik of Tomsk State University [Vestnik Tomskogo gosudarstvennogo universiteta]*, 352, 203–206. (In Russian).
- Convention on Biological Diversity. (1992). United Nations. Rio de Janeiro.
- Davydov, V.V., Timoshok, E.E. (2010). Forming of soils of the young moraines of the Aktru basin (Central Altai, Severo-Chuyskiy Range). *Contemporary Problems of Ecology*, 3 (3), 356–362. <https://doi.org/10.1134/S1995425510030161>.
- Dushkin, M.A. (1965). Long-term fluctuations of Aktru glaciers and conditions of development of young moraines. *Glatsyologiya Altaya [Glaciology of the Altai]*, 4, 83–101. (In Russian).
- Gureyeva, I.I., Timoshok, E.E. (2016). Ferns in the present-day periglacial zone of the Central Altai. *Contemporary Problems of Ecology*, 9 (1), 18–28. <https://doi.org/10.1134/S1995425516010054>

- IPNI. International Plant Names Index. Published on the Internet <http://www.ipni.org>, The Royal Botanic Gardens, Kew, Harvard University Herbaria & Libraries and Australian National Botanic Gardens. Accessed: 25.11.2020.
- Ivashkevich, B.A. (1929). Virgin forest, features of its structure and development. *Lesnoye khozyaystvo i lesnaya promyshlennost* [Forestry and forest industry], 10, 36–44; 11, 40–47; 12, 41–46. (In Russian).
- Kedrovye lesa Sibiri [*Siberian cedar forests*]. (1985). Novosibirsk: Nauka (In Russian).
- Komin, G.E. (2017). Terms in the theory of the forest forming process. *Lesovedeniye* [Forestry studies], 6, 457–463. <https://doi.org/10.7868/S0024114817060092> (In Russian).
- Krylov, A.G., Rechan, S.P. (1965). Forest zoning and forest types. *Lesa Gornogo Altaya* [Forest of Gornyi Altai]. Moscow: Nauka (In Russian).
- Krylov, G.V., Talantsev, N.K., Kozakova, N.F. (1983). *Cedar*. Moscow: Lesnaya promyshlennost Publ. (In Russian).
- Kuminova, A.V. (1960). Rastitelnyi pokrov Altaya [Vegetation cover of the Altai]. Novosibirsk: Siberian Branch of the USSR Academy of Sciences (In Russian).
- Ledniki Aktru (Altai) [The Glaciers of Aktru (the Altai)]. (1987). Leningrad: Gidrometeoizdat (In Russian).
- Lindholm, G. (1999). Conservation of old-growth forests in Finland. Indigenous forests of the taiga zone of Europe: current state and conservation problems. Petrozavodsk (In Russian).
- Okishev, P.A., Adamenko, M.F., Narozhny, Yu.K. (2000). Dynamics of glaciers and climate in the mountains of Southern Siberia. Regionalnyi monitoring atmosfery [Regional monitoring of the atmosphere]. Part 4. Natural and climatic changes. Tomsk, 164–199. (In Russian).
- Peterken, G.F. (1996). Natural woodland: ecology and conservation in northern temperate regions. Cambridge, New-York & Melburn: Cambridge Univ. Press.
- Polikarpov, N.P., Chebakova, N.M., Nazimova, D.I. (1986). *Klimat i gornyye lesa Yuzhnoi Sibiri* [Climate and mountain forests of South Siberia]. Novosibirsk: Nauka (In Russian).
- Pullin, A.S. (2002). Conservation Biology. Cambridge: Cambridge Univ. Press.
- Ramenskiy, L.G., Tsatsenkin, I.A., Chizhikov, A.N., Antipin, N.A. (1956). *Ekologicheskaya otsenka kormovykh ugodiy po rastitelnomu pokrovu* [Ecological assessment of forage lands by vegetation cover]. Moscow (In Russian).
- Sapozhnikov, V.V. (1901). *Katun i yeyo istoki: puteshestviya 1897–1899 godov* [Katun and its headwaters: travels of 1897–1899]. Tomsk: Parovaya topografiya P.I. Makushina (In Russian).
- Sevast'yanov, V.V. (1998) *Klimat vysokogornyykh rayonov Altaya i Sayan* [Climate of the high-mountain regions of the Altai and Sayan]. Tomsk: Tomsk State University (In Russian).
- Timoshok, E.E., Nikolaeva, S.A., Skorokhodov, S.N., Savchuk, D.A., Bocharov, A.Yu. (2009). Peculiarities of ontogenetic states within generative period of *Pinus sibirica* (Pinaceae) in forests of the Central Altai. *Rastitelnye resursy* [Plant resources], 45(1), 3–12. (In Russian).
- Timoshok, E.E., Skorokhodov, S.N., Timoshok, E.N. (2010). Flora of high-altitude forests of the upper reaches of the Aktru river (Severo-Chuyskiy Range, Central Altai). *Zhurnal Sibirskogo federalnogo universiteta. Biologiya* [Journal of Siberian Federal University. Biology], 4 (3), 351–371. (In Russian).
- Timoshok, E.E., Timoshok, E.N., Skorokhodov, S.N. (2014). Ecology of Siberian stone pine (*Pinus sibirica* Du Tour) and Siberian larch (*Larix sibirica* Ledeb.) in the Altai Mountain glacial basins. *Russian Journal of Ecology*, 45 (3), 194–200. <https://doi.org/10.1134/S1067413614030138>.
- Timoshok, E.E., Timoshok, E.N., Nikolaeva, S.A., Savchuk, D.A., Filimonova, E.O., Skorokhodov, S.N., Bocharov, A.Yu. (2016). Monitoring of high-altitude terrestrial ecosystems in the Altai Mountains. *IOP Conference Series: Earth Environmental Science*, 48 (1), 1–9. <https://doi.org/10.1088/1755-1315/48/1/012008>.
- Tipy lesov gor Yuzhnoi Sibiri [Types of forests in the mountains of South Siberia]. (1980). Novosibirsk: Nauka (In Russian).
- Tsatsenkin, I.A. (1967). *Ekologicheskiye shkaly dlya rasteniy pastbishch i senokosov gornyykh i ravninnykh rayonov Sredney Azii, Altaya i Urala* [Ecological scales for plants of pastures and hayfields of mountainous and lowland regions of Central Asia, Altai and the Urals]. Dushanbe: Donish (In Russian).
- Tsatsenkin, I.A., Savchenko, I.V., Dmitrieva, S.I. (1978). *Metodicheskie ukazaniya po ekologicheskoi otsenke kormovykh ugodii tundrovoi i lesnoi zon Sibiri i Dalnego Vostoka po rastitelnomu pokrovu* [Methodological Guidelines for Ecological Assessment of Rangelands by Plant Cover in the Tundra and Forest Zones of Siberia and the Far East], Moscow: Vses. Nauchno-Issled. Inst. Kormov, ... p. (In Russian).
- Vorobjev, V.N., Naroshny, Ju.K., Timoshok, E.E. et al. (2001). Ecological and biological studies in the upper reaches of the Aktru river in the Altai Mountains. *Glatsiologiya Sibiri* [Glaciology of Siberia], 274, 78–82. (In Russian).
- Vostochno-Evropeiskiy lesa: istoriya v golotsene i sovremennost [Eastern European forests: History in the Holocene and modernity]. (2004). Moscow: Nauka (In Russian).
- Zhukov, E.A. (2006). Old trees as part of the system of observations of climatic changes in the Altai-Sayan region. *Vychislitelnyye tekhnologii* [Computational technologies], 11 (2), 109–114. (In Russian).
- Zverev, A.A. (2007). *Information tekhnologii v issledovaniyakh rastitelnogo pokrova* Information technologies in research of vegetation cover. Tomsk: Publishing House TML-Press. (In Russian).

---

**Citation:**

Timoshok, E.E., Timoshok, E.N., Gureyeva, I.I. (2020). Ecological and cenotic features of the old-growth *Pinus sibirica* forests in the North-Chuya glaciation center, Russian Altai. *Ukrainian Journal of Ecology*, 10(6), 291–298.



This work is licensed under a Creative Commons Attribution 4.0. License